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# Sexual selection favors harmful mating in hermaphrodites more than in gonochorists

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**Synopsis** Hermaphroditic animals often exhibit mating mechanisms that seem more damaging than those in species with separate sexes. Our analyses indicate that this difference is real. While females only remate when the benefit is positive, hermaphrodites remate even when this implies losing female fitness. This occurs because hermaphrodites can outweigh losses in the female function by gaining paternity. In an extended model we ask whether this favors the evolution of more male harm in hermaphrodites. When male harm only suppresses remating in the receiver it neither evolves in hermaphrodites nor in gonochorists. However, when male harm is coupled to a fertilization advantage, it evolves in both forms of gender expression with the highest levels in hermaphrodites. Hence, hermaphrodites are more prone to be caught in costly escalations than gonochorists. We discuss the implications for the evolution of gender expression in animals and plants.

## Introduction

Sexual conflicts arise when reproductive interests of mating partners differ, which is usually the case in promiscuous species. Although females may benefit from being promiscuous (Jennions and Petrie 2000), this reduces the effectiveness of mating for males. To assure paternity, males may therefore attempt to suppress remating in their partners using mating plugs, mate guarding, and antiaphrodisiacs, or by inducing refractory periods physiologically or via a physical cost (Johnstone and Keller 2000). The resulting conflict between mates is well studied in animals with separate sexes (gonochorists) and can initiate costly coevolutionary arms races (Rice 1996; Arnqvist and Rowe 2002, 2005). Conversely, sexual conflict in hermaphrodites remains poorly understood.

Hermaphrodites allocate resources to a male *and* female function. This makes them ideally suited for environments in which mate availability and gender are unpredictable (Ghiselin 1969) or reproductive gains show diminishing returns in at least one gender (Charnov 1979). Yet, hermaphrodites also seem to face unusual problems. Especially internally fertilizing taxa often have strikingly complicated genital systems and matings frequently involve overt aggression or injurious mechanisms (Michiels 1999). For example, hypodermic insemination appears more prevalent and

radical among hermaphrodites (Michiels and Newman 1998) than gonochorists. It is widespread among hermaphroditic groups such as leeches, polyclad flatworms and sea slugs, whereas only a few cases are known among gonochorists (for example bedbugs: Stutt and Siva-Jothy 2001). Likewise, the transfer of allohormones (Koene and Ter Maat 2001, 2002), though present in gonochorists (Gillott 2002; Chapman and others 2003), seems to be taken to extremes in hermaphrodites. For example, sharp love darts (Koene and Chase 1998) and piercing setae (Koene and others 2002, 2005) have evolved to inject secretions directly into the receiver's body.

Here, we investigate whether the suspected difference between gonochorists and hermaphrodites is inherent to the mode of gender expression. We first demonstrate that hermaphrodites will accept additional matings, even when these reduce maternal fitness. We then go on to show that this can lead to the evolution of levels of male harm that exceed the expected level for gonochorists. The paradigm we use is a modified version of the model developed by Johnstone and Keller (2000), who investigated the evolution of male harm in gonochorists.

## Results

The models we develop here have a clear goal: to compare a gonochoric population to a hermaphroditic

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population in aspects of remating decision and male harm. These populations will be defined on an “all-else-being-equal” basis, meaning that both populations only differ in their gender expression, nothing else. We shall be looking for differences in stable values for key variables. Competition, coexistence or interbreeding between the 2 forms is not considered here, but will be considered elsewhere.

### Basic model

Consider 2 separate, equal-sized populations; 1 consisting of hermaphrodites with a 1:1 sex allocation, the other of gonochorists with a 1:1 sex ratio. Eggs are produced once in a lifetime (or independent reproductive episode). A hermaphrodite produces half the number of eggs a female produces, resulting in equal total fecundity in both populations. Fertilization is preceded by 1 or 2 inseminations with a random partner. Females and hermaphrodites can remate a single time after the first mating, depending on whether this increases their fitness. Males mate unconditionally when encountering a receptive female, but never mate more than twice. For simplicity, in hermaphrodites insemination is assumed reciprocal. In each mating, ejaculates have constant quality and quantity. Individuals do not distinguish virgins from singly mated partners.

### Decision rules for remating in gonochorists

We set female fitness 1 for a singly mated female. Let  $f$  be the female's fitness increase obtained when remating.  $f$  is taken from a probability distribution  $p(f)$ , for which we assume a normal distribution with mean  $\bar{f}$  and standard deviation  $s$ .  $f$  is not an inherited trait, but a phenotypic variable that describes how much fitness a female can expect to gain when remating. For instance, it could express the genetic quality of the second mate relative to the first. Here, we vary  $\bar{f}$  between  $-1$  (losing all fitness obtained in first mating) and  $1$  (doubling fitness). Since a doubly mated female has fitness  $1 + f$ , a female should remate when

$$1 < 1 + f \text{ or } f > 0. \quad (1)$$

Equation (1) suggests that females know the value of  $f$ . We actually only assume that females can optimize their remating likelihood to  $p(f)$  from here onward. Male reproductive success depends on the frequency of doubly mating partners in the population  $\rho$ , which can be calculated as

$$\rho = \int_c^\infty p(f)df \quad (2)$$

with  $c$  the smallest value of  $f$  for which females are prepared to remate ( $c = 0$  for females). The average

paternity a male can gain from a single mating  $m$  is given by the fitness of an average female divided by the expected number of matings per individual in the population ( $1 + \rho$ ). Average female fitness is the sum of the contribution from singly mated females and that from doubly mated females.

$$m = \frac{\int_{-\infty}^c p(f)df + \int_c^\infty (1+f)p(f)df}{1 + \rho}$$

which simplifies to

$$m = \frac{1 + \int_c^\infty f p(f)df}{1 + \rho}. \quad (3)$$

### Decision rules for remating in hermaphrodites

In hermaphrodites, female fitness and  $f$  are assumed to be only half of those in females, but total fitness is raised by paternity. Male fitness per mating is also only half that of a pure male  $m$ . Assuming a 1:1 sex allocation, a hermaphroditic individual should remate whenever

$$0.5 + 0.5m < 0.5 + 0.5f + m \quad (4)$$

or

$$m + f > 0 \Leftrightarrow m > -f \Leftrightarrow f > -m. \quad (5)$$

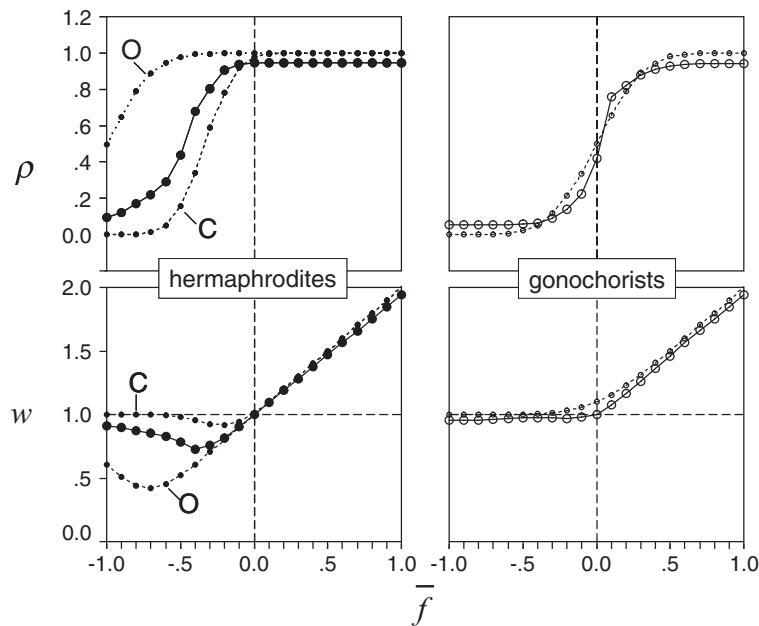
Hence, whenever the gain in one sex function exceeds the losses in the other, a hermaphrodite should remate. This simple, but important difference with gonochorists shows that whereas females will only remate when the expected benefit is positive, hermaphrodites will accept a loss in female fitness as long as it is compensated for by a larger gain in male fitness [compare Eqns. (1)–(5)]. Entering Eqn. (3) into (5) yields

$$f > -\frac{(1 - \rho) + \int_c^\infty (1+f)p(f)df}{1 + \rho} \quad (6)$$

with  $c = -m$ .

### Remating rates as a function of $\bar{f}$

For gonochorists, the proportion of individuals that remates  $\rho$  is easily calculated, because a female's remating decision only depends on her personal  $f$  value. In hermaphrodites, remating depends on remating decisions of other individuals, making Equations (3) and (6) inherently recursive. However, we can calculate upper and lower limits by entering extreme values for  $\rho$ . At the “optimistic” extreme, individuals base their remating decision on the assumption that no one else in the population remates (assumed  $\rho = 0$ ), eliminating sperm competition and thus maximizing the gain from remating. The decision rule for this case can



**Fig. 1** Remating rate  $\rho$  and mean fitness  $w$  as a function of mean female remating benefit  $\bar{f}$  for hermaphrodites (left, closed symbols) and females (right, open symbols). Large symbols result from a simulation for each  $\bar{f}$  with  $s = 0.25$  (Appendix, Model A). Small symbols were calculated by randomly drawing  $f$  10,000 times from a normal distribution with  $\bar{f}$  and  $s = 0.25$ , followed by a calculation of the remating decision using Equations (1) and (6). For hermaphrodites the 2 extremes are shown. Curve O shows the optimistic extreme when animals assume that the rest of the population will not remate. Curve C shows the most conservative assumption that all others remate (see text).  $w = 1$  is for populations in which all individuals mate exactly once. For higher or lower values of  $s$ , the curves are horizontally stretched or compressed around 0 without affecting observed trends.

be simplified from Equation (6) to  $f > -1$  (Fig. 1, curve O). At the “conservative” extreme individuals assume that all other individuals mate twice (assumed  $\rho = 1$ ), maximizing sperm competition and minimizing the possible gain from remating for the male function (Fig. 1, curve C). Under this condition, Equation (6) can be simplified to  $f > -0.5(1 + \bar{f})$ . The remating likelihood for the focal individual is then given by Equation (2) with  $c = -0.5(1 + \bar{f})$ . Average individual fitness  $w$  is based on the definitions presented above for singly and doubly mated females and hermaphrodites (Fig. 1, lower row). The average fitness of pure males is identical to that of pure females.

Given that an analytical ESS solution is not straightforward for hermaphrodites, we calculated the optimal remating rate using an evolutionary algorithm (Wilson 2000). Here,  $\delta$  is defined as an evolvable, variable trait expressing the likelihood that an individual will remate.  $\delta$  is allowed to evolve across generations until a stable (ESS) value is found. The overall remating rate in the population  $\rho$  is directly calculated from the effective number of individuals that remates (Appendix, Model A). The simulation was also performed for gonochorists as a control for the calculated values. Figure 1 confirms that hermaphrodites are indeed generally prepared to remate at the expense of female

fitness, corresponding to negative  $f$ -values. Even if hermaphrodites would base their remating decision on the most conservative assumption (assumed  $\rho = 1$ ), they remate more readily than gonochorists for  $\bar{f}$  around or below 0.

### Including male harm

Given the intrinsic tendency to accept high female mating costs, we now ask whether hermaphrodites are also more likely to evolve harmful male tactics than male gonochorists. The level of male harm is denoted as  $t$ . The resulting cost for the recipient is assumed to be an accelerating function of  $t$  of the general form  $t^a$  with  $a > 1$  (see Johnstone and Keller 2000 for rationale). Combining this with Equation (1) leads to the prediction that females should remate when

$$1 - t_r^a < 1 + f - (t_r + \bar{t})^a \quad (7)$$

or

$$f > (t_r + \bar{t})^a - t_r^a \quad (8)$$

in which  $t_r$  is the male harm received during the first copulation and  $\bar{t}$  the population average expected for the second mating. If we assume that  $t_r = \bar{t}$ , the critical (that is minimal) amount of  $t$  required to prevent a female

from remating ( $t_c$ ) is obtained by setting the fitness of individuals that mate once and twice equal in Equation (7) and solving for  $t$ :

$$t_c = \sqrt[a]{f/(2^a - 1)}. \quad (9)$$

The expected paternity from a single mating for a male  $m$  changes from Equation (3) into

$$m = \frac{(1-\rho)(1-t^a) + \int_c^\infty (1+f-(t+\bar{t})^a)p(f)df}{1+\rho}. \quad (10)$$

In hermaphrodites the cost inflicted by the “male” partner equals half that in gonochorists. Applying this to Equation (4) leads to the prediction that hermaphrodites should remate whenever

$$0.5 - 0.5t_r^a + 0.5m < 0.5 + 0.5f - 0.5(t_r + \bar{t})^a + m \quad (11)$$

or

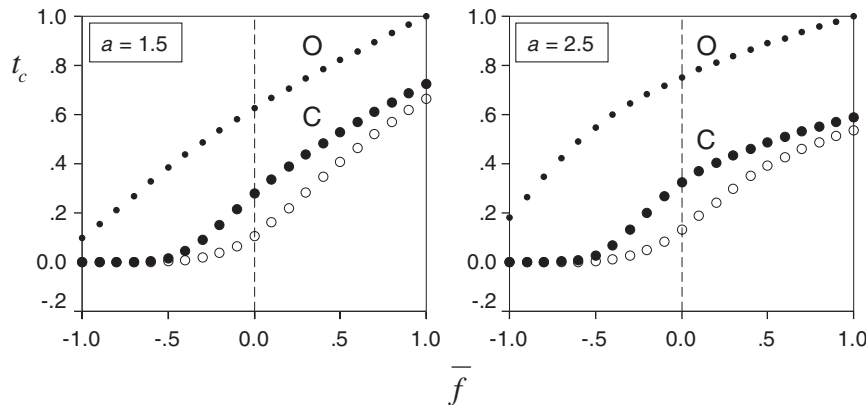
$$f > (t_r + \bar{t})^a - t_r^a - m. \quad (12)$$

Because calculation of  $m$  is recursive, a direct calculation of  $t_c$  is only possible for extreme values of the (assumed) remating rate among other individuals in the population ( $\rho$ ). For  $\rho = 0$ , Equation (10) changes into  $m = 1 - t^a$ . Inserting this into Equation (11) and solving for  $t = t_r = \bar{t}$  results in

$$t_c = \sqrt[a]{\frac{1+f}{2}}. \quad (13)$$

For  $\rho = 1$ , Equation (10) can be rewritten as  $m = \frac{1+f-(2t)^a}{2}$ , leading to

$$t_c = \sqrt[a]{\frac{1+2f+\bar{f}}{3(2^a-2)}}. \quad (14)$$



**Fig. 2** Critical levels of male harm  $t_c$  ( $t$ -value for which singly and doubly mated individuals have the same fitness) as a function of the mean remating benefit  $\bar{f}$  for females (open circles) and hermaphrodites (O = most optimistic and C = most conservative estimate, see Fig. 1). Calculations were performed, as in Figure 1, by randomly drawing  $f$  10,000 times from a normal distribution for each  $\bar{f}$  with  $s = 0.25$ , followed by a calculation of  $t_c$  using Equations (9), (13) and (14). Averages per  $\bar{f}$  are shown (Appendix, Model B).

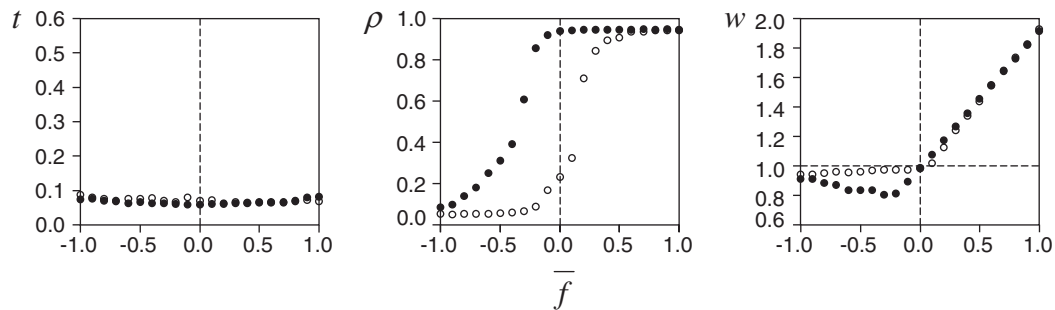
Using Equations (9), (13), and (14) on 10,000 randomly drawn individuals for each value of  $\bar{f}$ , we calculated the average  $t_c$ . Expressions (9), (13), and (14) only yield a solution for individuals that would have remated in the absence of  $t$ . We set  $t_c = 0$  for individuals for which this was not the case, because they did not require male harm to prevent them from remating. Figure 2 confirms that more male harm is required to keep a hermaphrodite from remating than a gonochorist. This is also true across a wide range for (assumed)  $\rho = 1$ , a condition under which remating is least profitable for hermaphrodites. The difference is particularly strong around  $\bar{f} = 0$ . This range coincides with modest benefits or costs of remating, which is probably most realistic. However, Figure 2 does not yet prove that male harm will evolve.

#### Male harm evolution without sperm precedence advantage

It is presumed that sperm donors harm their mates as a negative pleiotropic side effect of adaptations that give males a reproductive advantage over other males (Morrow and others 2003). This implies that harming females is not adaptive per se, but a collateral cost of male-male competition (Rice 1996; Chapman and others 2003). Johnstone and Keller (2000), however, predict that under certain conditions, a male may also benefit from harming its partner when the only consequence is that it prevents the female from remating, without a relative fertilization advantage. Here, we use a simulation approach to investigate whether male harm does indeed evolve in the absence of a fertilization advantage and ask whether the effect is stronger in hermaphrodites than in gonochorists.

We extended our evolutionary algorithm by including  $t$  as an evolvable trait (Appendix, Model B).





**Fig. 3** Simulated evolutionary stable levels of male harm  $t$  without fertilization advantage as a function of  $\bar{f}$  with  $s = 0.25$  and  $a = 2$ . Points show averages of 5 independent simulation runs in hermaphrodites (closed circles) and gonochorists (open circles) (Appendix, Model B).

For now, we assume that  $t$  only affects the remating decision of the recipient and confers no additional fertilization advantage to the donor. Figure 3 shows that under these conditions, male harm evolves in neither hermaphrodites nor gonochorists. The same outcome was obtained when the first generation was initialized with high starting values for  $t$ . Hence, the lack of evolution of male harm  $t$  was not due to attraction to zero in the vicinity of zero, as suggested for some part of the parameter space by Johnstone and Keller (2000). Not surprisingly, remating rates and fitness values are very similar to the basic model (Fig. 1). Because results were identical for all values of last-male precedence ( $P_2$ ), averages are shown. Hence, under the current paradigm, reducing a female's fitness in order to keep it from remating is insufficient to explain the evolution of male harm.

#### Male harm evolution with sperm precedence advantage

In an alternative version of the algorithm, male harm not only affects the remating decision of the female, but also affects the donor's sperm precedence advantage relative to a previous or later competitor. For this purpose, we multiplied  $P_2$  (proportion offspring sired by second male partner) with the ratio of  $t$  from the second donor over that from the first donor. The result was limited to  $0 \leq P_2 \leq 1$ . This introduces a paternity advantage for the donor who applies relatively more harm. Simulation results differed for different initial  $P_2$  values, but were identical for corresponding  $P_2$  and  $(1 - P_2)$  values (symmetry around  $P_2 = 0.5$ ). Data are shown for 3 categories of  $P_2$  and  $a = 2$ . Figure 4 shows that higher levels of  $t$  evolve for higher values of  $\bar{f}$  and intermediate  $P_2$ -values. In hermaphrodites  $t$ -levels are higher than in gonochorists for  $\bar{f}$  around zero. Hence, including a sperm precedence advantage (1) allows male harm to evolve and (2) again shows the predicted difference between hermaphrodites and gonochorists. Note that fitness

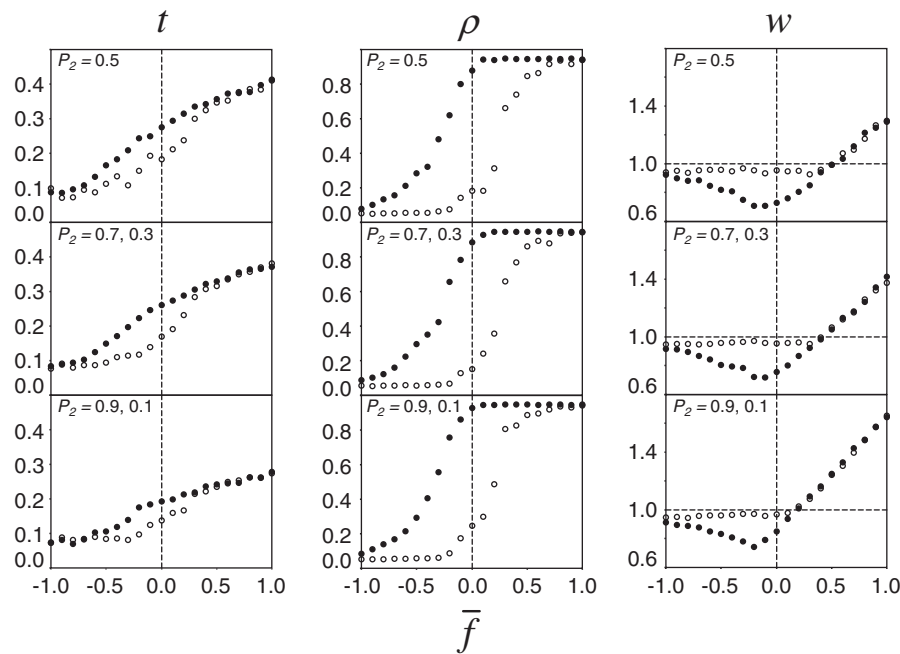
losses due to  $t$  are strongly amplified in hermaphrodites due to their elevated remating rate for low values of  $\bar{f}$ . Simulations were tested for a wider range of parameter values for  $s$  and  $a$  (including a linear cost function with  $a = 1$ ). The qualitative differences between hermaphrodites and gonochorists shown here were always present.

## Discussion

Our analyses illustrate 2 important differences between hermaphrodites and gonochorists when compared on an "all-else-being-equal" basis. First, hermaphrodites are inherently more likely to accept higher mating costs. They will remate as long as paternity outweighs the fecundity cost paid by the female function. This is a robust difference that is independent of the presence or absence of male harm or the details of the paradigm used [Eqn. (1) and (5)]. Second, when explicitly coupled to a fertilization advantage, male harm evolves and reaches higher levels in hermaphrodites than in gonochorists. Yet, lower fitness in hermaphrodites is to a large extent due to their intrinsic preparedness to remate at the expense of the female function and only to a lesser extent to the cost of male harm per se. The difference between hermaphrodites and gonochorists is largest for female remating benefits ( $\bar{f}$ ) around 0, that is small benefits and costs for remating in the female function.

#### Robustness of the results

The observed difference between the 2 forms of gender expression is a conservative estimate because only harm to the female function was considered. In contrast to males, hermaphrodites may target the male rather than the female function of their partners. Damaging the male function of the partner may reduce the remating rate in a hermaphrodite without affecting its female fecundity. Although there is evidence for this (for example in penis-biting



**Fig. 4** Simulated evolutionary stable levels of male harm  $t$  in hermaphrodites (filled circles) and gonochorists (open circles), with the corresponding remating rate  $\rho$  and average fitness  $w$  as a function of  $\bar{f}$  with  $s = 0.25$  and  $a = 2$ . The  $P_2$ -values are indicated. Note that the actual cost paid by the receiver is  $t^a$  (for example 0.09 for  $t = 0.3$ ) (Appendix, Model B).

slugs: Reise and Hutchinson 2002) harming the male function was not considered here, as it is a form of male-male competition, which cannot take place between a female and male sexual partner. Preliminary simulations show that harm to the male function in hermaphrodites always rapidly evolves to very high levels (not shown).

Under natural conditions, sex allocation and sex ratio are likely to diverge from the 1:1 ratio that we assumed here. Here, we fixed sex allocation and sex ratio only to keep hermaphrodites and gonochorists comparable. Unpublished analyses with another simulation approach (N. K. Michiels and V. S. Brauer, unpublished data) suggest that male harm will strongly reduce mating rate in systems where individuals can mate more than twice. This will reduce their allocation to the male function and lead to increased egg production. As a result, compensatory changes in sex allocation may actually buffer the fitness costs of male harm in hermaphrodites to a larger extent than suggested by the current paradigm. Yet, the qualitative effect described here is also present in these other simulations (models by N. K. Michiels and V. S. Bauer).

### All-else-being-equal

Although the difference between hermaphroditism and gonochorism is prominent when compared under otherwise identical conditions, natural mating conditions are likely to differ between the 2 types.

Hermaphroditism is particularly stable under low mating rates (Charnov and others 1976, Puurtinen and Kaitala 2002). This may reduce the likelihood that mating conflicts escalate. Low mating rates also favor a female biased sex allocation (for example Fischer 1981; Greeff and others 2001) giving hermaphroditic populations a potential fecundity advantage. In systems where selfing is a viable alternative to outcrossing, partial selfing may also slow down escalation.

The fact that hermaphroditism is often associated with slow-moving animals with limited communication abilities and low mating rates, whereas gonochorism is more prevalent in communicative animals with usually higher mating rates and complicated mating rituals makes an empirical test of our results very difficult: an “all-else-being-equal” situation is very rare in nature. And if so, no studies to date present mating rates and female fecundity for such sibling systems. Finding a system of at least 2 outcrossing, internally fertilizing sister species that only differ in their mode of gender expression is an important challenge for the future.

### Consequences for plant biology

Our model also applies to plants. Dioecious (hermaphroditic) flowers often remain receptive for pollinators after all ovules are fertilized. This is advantageous for the pollen-producing function, but goes at the expense of female fecundity, as pollinators can damage

female structures (Herre and West 1997) or introduce parasites (Roy 1994). Embryos may even be aborted to increase pollen output (Burd and Callahan 2000). Hence, at least in certain cases hermaphroditic plants seem to sacrifice part of their female function in exchange for fatherhood, which merely rephrases our conclusions for animals.

### Relative fertilization advantage: required or not

In Johnstone and Keller's model without sperm precedence advantage certain combinations of parameters ( $\bar{f}$ ,  $s$ ,  $a$ ) yielded an evolutionary stable value for  $t$ , but  $t = 0$  was also stable for part of the parameter range. Our simulation of male harm without a sperm precedence advantage suggests that  $t \approx 0$  is the only solution. But this does not imply that the evolution of male harm is not possible when the only effect is suppression of remating in the receiver. The paradigm used here possibly underestimates the benefits of remating suppression in 2 ways.

First, sperm receivers never copulate more than twice, maximizing the likelihood that a sperm donor meets a partner that will not remate anyway. Harming a mate that will not remate always leads to a reduction in male fitness and is therefore maladaptive. Suppression of remating may become more adaptive when the reproductive history of a partner is known (virgin or mated) and individuals can mate more than twice. Second, in our simulation the likelihood of remating was defined as an individual trait  $\delta$ , which coevolved with male harm  $t$ . Hence, we refrained from using a decision rule based on the  $t$  effectively used by the partner as in Johnstone and Keller's model. Instead, remating decisions depended on the value of an individuals' intrinsic likelihood to remate ( $\delta$ , see Appendix). Leaving the decision rule out of the simulation and allowing  $\delta$  to evolve toward its own optimum in the model offers the advantage that the simulation is independent of any a priori defined decision rule—providing an independent control. It makes the simulation also more basic since it does not assume that individuals have the ability to assess their (first or second) partners and change their remating decision accordingly. The latter point in particular may explain why our simulation yields different results from the analytical solution proposed by Johnstone and Keller (2000).

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## Appendix

### Model A: basic version

We used an evolutionary algorithm (Wilson 2000) to find ultimately stable values for the proportion of remating individuals in the population  $\rho$ . We generated 2 separate populations of 1000 individuals, 1 hermaphroditic and 1 gonochoric, the latter consisting of 500 females and 500 males. For each hermaphrodite and female an  $f$ -value was randomly drawn from a normal distribution with  $\bar{f}$  and  $s = 0.25$ , limited to  $\bar{f} \pm 3s$ . Since  $f$  is not inherited, this was repeated each generation. In the first generation of a run, individuals obtained a probability of remating  $\delta$  randomly drawn from a narrow, normal distribution with  $\bar{\delta} = 0$  and  $s = 0.1$ , truncated at 0 and 1. Mating partners were picked randomly. Virgin females and hermaphrodites mated unconditionally with the first receptive random partner. After mating once, individuals were removed from the mating pool with a likelihood of  $1 - \delta$ . Individuals were always removed after the second mating. This also applies to males. Fitness

for singly and doubly mated individuals was calculated as described above [see for example Eqns. (7) and (11)]. When female fitness was negative (for example after remating despite a low, negative  $f$ ), it was reset to 0. The fitness of sperm donors was set identical to the female fitness of their mate(s), adjusted for their paternity share in doubly mated partners using a fixed value for last-male paternity ( $P_2$ ). After completion of the mating round, we calculated the population average  $\bar{\delta}$ , weighted for individual fitness. This weighted  $\bar{\delta}$  was used to seed the next adult generation. Using a weighted average to seed the next generation rather than producing offspring and generating the next generation from these, dramatically reduced stochasticity and processing time, while keeping the results identical. Simulations were run for 2000 generations with  $s = 0.1$  for  $\bar{\delta}$  and ended with another 3000 generations with  $s = 0.02$ . This procedure allowed for bigger evolutionary steps during the first 2000 generations, with smaller steps and lower variance in the last 3000 steps. Stable  $\bar{\delta}$ -values were always reached well before the end of the 5000 generations. We repeated runs for values of  $P_2$  (0 to 1) and  $\bar{f}$  (–1 to 1) in steps of 0.1. We also tested the effects of changing  $s$  for  $\bar{f}$ , but only show data for  $s = 0.25$  throughout. Decreasing or increasing  $s$  merely compressed or stretched the graphs horizontally. Each combination of parameter values was tested in 5 independent runs and results were averaged.

### Model B: inclusion of male harm

As in A, but now all individuals also obtained a  $t$ -value drawn from a normal distribution with mean  $\bar{t}$  equal to the average of  $t$ -values from the previous generation (weighted by fitness) and a standard deviation of  $s = 0.1$  reducing to 0.02 after 2000 generations.  $t$  was drawn such that  $t > 0$  because of a division by zero that would otherwise occur in the calculation of relative paternity. The latter was calculated by multiplying  $P_2$  by the ratio of  $t$  from the second partner over  $t$  from the first partner. The result was limited to  $0 \leq P_2 \leq 1$ . Individual  $t$ -values and individual fitness allowed calculation of a weighted  $\bar{t}$  that was used to seed the next adult generation. Results are shown only for  $a = 2$ . Since  $t < 1$  in all runs, increasing  $a$  resulted in a strong decrease in the cost resulting from male harm ( $t^a$ ). This did not lead to an appreciable increase in the evolved level of male harm, but led to increased fitness instead.